The ticks (Acari: Ixodida: Argasidae, Ixodidae) of Paraguay

S. NAVA*, M. LARESCHI†, C. REBOLLO‡, C. BENÍTEZ USHER⁵, L. BEATI¶, R. G. ROBBINS**, L. A. DURDEN¶, A. J. MANGOLD* and A. A. GUGLIELMONE*

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The ticks reported in Paraguay, which are here reviewed, can be categorized as 'endemic or established' (Argas persicus or a sibling species, Ornithodoros hasei, O. rostratus, O. rudis, O. talaje/O. puertoricensis, Amblyomma aureolatum, Am. auricularium, Am. brasiliense, Am. cajennense, Am. calcaratum, Am. coelebs, Am. dissimile, Am. dubitatum, Am. incisum, Am. longirostre, Am. nodosum, Am. ovale, Am. pacae, Am. parvum, Am. pseudoconcolor, Am. rotundatum, Am. scutatum, Am. tigrinum, Am. triste, Dermacentor nitens, Haemaphysalis juxtakochi, H. leporispalustris, Ixodes loricatus, Rhipicephalus microplus, and Rh. sanguineus), 'probably endemic or established' (Ar. miniatus, Ar. monachus, Am. argentinae, Am. humerale, Am. naponense, Am. oblongoguttatum, Am. pseudoparvum, I. aragaoi/I. pararicinus, I. auritulus, I. luciae), or 'erroneously reported from Paraguay'(O. coriaceus, Am. americanum and Am. maculatum). Most Paraguayan tick collections have been made in the Chaco phyto–geographical domain, in the central part of the country. Argas persicus or a related species, Am. cajennense, D. nitens, Rh. microplus and Rh. sanguineus are important parasites of domestic animals. Ornithodoros rudis, Am. aureolatum, Am. brasiliense, Am. cajennense, Am. coelebs, Am. incisum, Am. ovale and Am. tigrinum have all been collected from humans. In terms of public health, the collections of Am. cajennense and Am. triste from humans may be particularly significant, as these species are potential vectors of Rickettsia rickettsii and Ri. parkeri, respectively.

Ticks (suborder Ixodida, superfamily Ixodoidea) are large, obligately haematophagous mites that, in some or all of their post-embryonic stages, are ectoparasites, infesting all classes of vertebrates except fish. Several species are vectors of agents that may cause disease in, or even kill, their hosts, and even uninfected ticks may cause dermatoses, envenomization, exsanguination or paralysis. Most research on

Neotropical ticks has been focused on those species of importance to livestock, especially the cattle tick *Rhipicephalus* (formerly *Boophilus*) *microplus* (Canestrini). Recent outbreaks of tick-transmitted human rick-ettsiosis in Argentina (Ripoll *et al.*, 1999), Brazil (Silva and Galvão, 2004) and Uruguay (Venzal *et al.*, 2004) have, however, generated renewed interest in the importance of ticks as vectors of human pathogens, and ticks are also excellent subjects for studies of regional biodiversity (Estrada-Peña *et al.*, 2005; Labruna *et al.*, 2005).

Reprint requests to: S. Nava. E-mail: snava@rafaela.inta.gov.ar; fax: +54 3492 440114.

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^{*}Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Rafaela, CC 22, CP 2300 Rafaela, Santa Fe, Argentina

[†]Centro de Estudios Parasitológicos y de Vectores, 2 N° 584, CP 1900, La Plata, Argentina

[‡]Parasitology Department, Faculty of Veterinary Sciences, San Lorenzo, Paraguay

[§]Consult-pec, José D. López 200, Asunción, Paraguay

[¶]United States National Tick Collection, Institute of Arthropodology and Parasitology and Department of Biology, Georgia Southern University, Statesboro, GA 30460-8056, U.S.A.

^{**}Defense Pest Management Information Analysis Center, Armed Forces Pest Management Board, Walter Reed Army Medical Center, Washington, DC 20307-5001, U.S.A.

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TABLE 1. The tick collection sites in each department of Paraguay, with their geographical co-ordinates

Department and collection site	Co-ordinates
ALTO PARAGUAY	
Cerro León	20°20′S, 60°20′W
Parque Defensores del Chaco	20°14′S, 60°12′W
ALTO PARANÁ	
Ciudad del Este	25°32′S, 54°37′W
BOQUERÓN	
Colonia Fernheim	22°14′S, 59°50′W
Colonia Mennonita SW	22°34′S, 59°56′W
Colonia Neuland	22°39′S, 60°07′W
Estancia Campo-í	22°12′S, 60°31′W
Estancia Faro Moro	21°42′S, 60°01′W
Filadelfia	22°20′S, 60°02′W
Filadelfia East	22°20′S, 59°20′W
Loma Plata	22°22′S, 59°51′W
Mariscal Estigarribia	22°01′S, 60°37′W
Toledo	22°07′S, 60°16′W
Transchaco Road km 580-620	21°10′S, 61°40′W
Villa de San Pedro	23°00′S, 60°00′W
CAAGUAZÚ	
Caaguazú	25°28′S, 56°01′W
Coronel Oviedo	25°27′S, 56°25′W
Yhu	24°58′S, 55°59′W
CENTRAL	
Asunción	25°16′S, 57°40′W
Estancia Surubí-y	25°10′S, 57°30′W
Guarambaré	25°29′S, 57°27′W
Luque	25°15′S, 57°29′W
San Lorenzo	25°20′S, 57°30′W 25°30′S, 57°33′W
Villeta CONCEPCIÓN	25 50 8, 57 55 W
Maldonado Cué	22°43′S, 56°49′W
Puerto Cooper	23°03′S, 57°43′W
Puerto Max	22°38′S, 57°46′W
Puerto Río Negro	23°25′S, 57°20′W
Río Apa	22°10′S, 57°50′W
Villasana	22°49′S, 57°06′W
CORDILLERA	22 19 0, 91 00 11
San Bernardino	26°16′S, 57°19′W
Sapucai (probable)	25°19′S, 56°55′W
GUAIRÁ	23 13 0, 30 33
Mbocayaty	25°43′S, 56°25′W
Villarica	25°46′S, 56°27′W
ITAPÚA	
General Artigas	26°56′S, 56°13′W
Río Pirapó area	26°54′S, 55°30′W
MISIONES	, "
San Ignacio	26°53′S, 57°02′W
San Juan Bautista	26°40′S, 57°09′W
ÑEEMBUCÚ	,
Garay Cué	26°25′S, 57°49′W
General Díaz	27°10′S, 58°25′W
San Fernando	26°35′S, 58°07′W
Yacaré	27°04′S, 57°25′W

TABLE 1. Continued

Department and collection site	Co-ordinates		
PARAGUARí			
Estancia Barrerito	26°24′S, 57°12′W		
Estancia Naranja-y	26°00′S, 57°00′W		
Paraguarí	25°37′S, 57°09′W		
Quindy	25°58′S, 57°13′W		
Sapucai	25°40′S, 56°57′W		
PRESIDENTE HAYES			
Chaco Experimental Station	23°40′S, 59°00′W		
Colonia Risso	22°21′S, 57°50′W		
Estancia Ninfa	24°46′S, 58°20′W		
Estancia San Rafael	24°12′S, 57°19′W		
Fortín Juan de Zalazar	23°06′S, 59°18′W		
Pozo Colorado	23°26′S, 58°51′W		
Rancho Alegre	23°45′S, 57°26′W		
San Bernardo	24°49′S, 58°40′W		
San Salvador	22°51′S, 57°48′W		
SAN PEDRO			
San Pedro	24°07′S, 56°59′W		

Given that animal husbandry is so vital to the economy of Paraguay (Payne and Osorio, 1990), a land-locked area with a diverse autochthonous fauna, it is surprising that this country's ticks remain little known, the only comprehensive review being that of Massi Pallarés and Benítez Usher (1982). In recent years, the examination of extant collections of Paraguayan ticks and the collection of additional specimens from various sites have permitted the present, critical review of the country's tick fauna. New information on hosts, distribution and ecology, that should prove useful in assessing the impact of these ectoparasites on human and 'animal' health, is presented below.

MATERIALS AND METHODS

The phylogenies followed for the present review were those of Barker and Murrell (2002) for the family Ixodidae, and of Hoogstraal (1985) for the Argasidae. Although there has been a more recent review of the taxonomy of argasid ticks (Klompen and Oliver, 1993), this was based



FIG. 1. The administrative divisions of Paraguay, showing the departmental borders.

almost entirely on morphological characters, with minimal consideration of biology, hosts, distribution, and molecular systematics (Guglielmone *et al.*, 2005), and is not followed here.

The present review is based on: (1) recent collections of ticks — currently deposited in the United States National Tick Collection (USNTC; Georgia Southern University, Statesboro, GA) or the tick collection of Nacional the Instituto de Tecnología Agropecuaria (INTA) at Rafaela, Argentina - from several hosts and localities in Paraguay; (2) the examination of unidentified Paraguayan specimens deposited in the tick collection of the Departamento de Entomología (TCDE) of the Museo de La Plata (Universidad de La Plata, La Plata, Argentina); (3) the unpublished records of Paraguayan ticks already in the USNTC; and (4) a thorough appraisal of the relevant

scientific literature. Whenever appropriate, the recorded names of mammalian hosts have been changed to accord with those used by Wilson and Reeder (1993).

The Paraguayan tick fauna is here discussed under three headings: 'endemic or established species', 'species probably endemic or established', and 'species erroneously reported as present in Paraguay'. No summary remarks on tick families and genera are included here because these have recently been published (González Acuña and Guglielmone, 2005). Unless otherwise noted, the known world distribution of each species is that described by Guglielmone *et al.* (2003*a*).

The collection localities for each tick species are listed in the text and the Table. Figure 1 shows the administrative divisions of Paraguay, and Figure 2 depicts the broad phyto–geographical divisions of the country,



FIG. 2. The phyto-geographical divisions of Paraguay. The phyto-geographical provinces of Cerrado and Paranaense belong to the Amazonic domain whereas Chaco province is within the Chaco domain.

according to Cabrera and Willink (1973) and Adámoli (1985).

Paraguay's phyto-geography comprises the Amazonic and Chaco domains. The Amazonic domain is represented by the Cerrado phyto-geographical province (CePP) in the north-east and by the Paranaense phyto-geographical province (PaPP) in the east (Fig. 2). The CePP, which covers the northern part of Amambay department and the easternmost parts of Concepción department (Fig. 1), is characterised by an annual rainfall of 1200-2000 mm (most of which falls in October-April), mean annual temperatures between 21°C and 25°C, and a landscape of open forest, with trees rarely taller than 12 m. The PaPP, which covers the entire departments of Canindeyú, Alto Paraná, Itapúa, Caazapá, the east-central parts of the departments of Misiones, Guairá and Caaguazú, and the eastern part of the San

Pedro department, is characterised by a yearly rainfall of 1500-2000 mm (most of which falls in November-March), mean annual temperatures between 16°C and 22°C, and a mountainous terrain, with subtropical rainforests as the dominant vegetation. The Chaco domain is only represented by one phyto-geographical province, known as the Chaco phytogeographical province (ChPP), but this covers all of central and western Paraguay (Fig. 2). The ChPP is chiefly distinguished by its generally flat terrain and a continental climate, with mean annual temperatures varying between 20°C and 23°C and annual rainfall increasing from west (500–800 mm, concentrated in the summer months of November-March) to east (800–1200 mm, with no seasonal peak). Trees of the genera Schinopsis, Aspidosperma and Caesalpinia are common in the ChPP.

RESULTS

Endemic or Established Tick Species

ARGASIDAE Canestrini

Argas Latreille; Argas persicus (Oken). Kohls et al. (1970) found females, nymphs and larvae of this tick species in a chicken house in Filadelfia, located in the ChPP. Argas persicus is a Palearctic species but specimens indistinguishable from this taxon have also been found in Argentina, Brazil and Cuba. It is possible that these Neotropical 'Ar. persicus' actually represent a sibling species.

Ornithodoros Koch; *Ornithodoros* hasei (Schulze). The USNTC contains specimens identified as Orn. hasei under accession numbers RML 064769 [three larvae, ex Noctilio leporinus, Fortín Juan de Zalazar, 25 September 1973, collector (coll.) R. L. Martin], and RML 064770 (two larvae, ex Noctilio leporinus, Fortín Juan de Zalazar, 27 September 1973, coll. R. L. Martin). These are the first Paraguayan records of Orn. hasei (the collection locality lies within the ChPP), a species that ranges from southern Mexico to Uruguay and the Caribbean islands. Jones et al. (1972) observed morphological variation among specimens from different localities and concluded that more than one species may be represented in material currently classified as Orn. hasei.

Ornithodoros rostratus Aragão. Massi Pallarés and Benítez Usher (1982) recorded this species from *Panthera onca* at Mariscal Estigarribia, and Keirans (1985) mentions males and a female from an unknown host in San Salvador. The USNTC contains RML 105928 (two males, host unknown, Filadelfia, June 1975, coll. K. Colin). The collection localities are all within the ChPP. *Ornithodoros rostratus* is also known from Argentina, Bolivia and Brazil.

Ornithodoros rudis Karsch. Massi Pallarés and Benítez Usher (1982) found this species on the ground at Colonia Fernheim. There are three collections in the USNTC: RML

015480 (six males and 13 females, host and locality unknown, October 1928, coll. E. Brumpt), RML 032661 (one male and one female, Asunción, host, date and collector unknown), and RML 065652 (13 nymphs identified as 'probably *Orn. rudis*', human, Loma Plata, 10 March 1975, coll. R. G. Unruh). Colonia Fernheim, Asunción and Loma Plata all lie within the ChPP. *Ornithodoros rudis* is also known from Brazil, Colombia, Ecuador, Panama, Peru and Venezuela.

Ornithodoros (Guérin-Méneville)/ talaje Ornithodoros puertoricensis Fox. Cordero et al. (1928) found adults of Orn. talaje in a chicken house in Asunción, and Keirans (1985) identified males, females and nymphs, from an unknown host, at the same locality. The USNTC contains RML 105921 (two larvae, ex Oryzomys sp., Transchaco Road km 580–620, 3 February 1978, coll. T.W. Nelson). The TCDE (accession GR038) contains a single nymph, collected in a chicken house in Villarica (date and collector unknown). All collection localities for this species lie within the Although Capriles and Gaud (1977) reported Orn. puertoricensis from Paraguay, this record requires confirmation because only the larvae of Orn. talaje and Orn. puertoricensis are readily separable by morphology (Kohls et al., Ornithodoros talaje has also been reported from Argentina, Brazil, Ecuador (Galapagos Islands), Guatemala, Uruguay and the Nearctic Region, while there are records of Orn. puertoricensis from southern Mexico, Nicaragua, Surinam and the islands of the Greater and Lesser Antilles. Both species have been found in Colombia, Panama and Venezuela.

IXODIDAE Murray

Amblyomma Koch; Amblyomma aureolatum (Pallas). Keirans (1985) confirmed the presence of Am. aureolatum (under the name Am. striatum) on cattle and humans in San

Pedro (ChPP). This species, whose adults chiefly infest Carnivora, has also been found in Argentina, Brazil, French Guiana, Surinam and Uruguay (Guglielmone *et al.*, 2003*c*).

Amblyomma auricularium (Conil). Massi Pallarés and Benítez Usher (1982) reported this tick from the armadillos Dasypus novemcinctus in Caaguazú, Euphractes sexcinctus in General Díaz and Puerto Río Dasypus semptemcinctus Presidente Hayes, and Tolypeutes mataco in an unknown site. The known distribution of Am. auricularium in Paraguay thus includes both the PaPP and the ChPP. This tick ranges from northern Patagonia (Argentina) northward throughout the Neotropics and (Nearctic) into the southern U.S.A. (Guglielmone et al., 2003b). It may be difficult to distinguish the males of Am. auricularium and Am. pseudoconcolor because, in the latter species, the scutal ornamentation (a crucial diagnostic character) is often indistinct (Jones et al., 1972).

Amblyomma brasiliense Aragão. Dios and Knopoff (1930) reported this species from undetermined hosts in Asunción, whereas Keirans (1985) recorded it from humans and cattle in San Pedro (ChPP). Outside Paraguay, Am. brasiliense is also known from Argentina and Brazil.

Amblyomma cajennense (Fabricius). Tonelli Rondelli (1937), Quinlan et al. (1980), Massi Pallarés and Benítez Usher (1982), Keirans (1985) and Walter (1990) reported Am. cajennense from a variety of hosts in Ciudad del Este, Colonia Neuland, Colonia Risso, Estancia Ninfa, Estancia San Rafael, Filadelfia, Filadelfia East, Garay Cué, Maldonado Luque, Cué, Estigarribia, Pozo Colorado, Rancho Alegre, San Bernardo, San Fernando, San Pedro, Toledo, 'Santa Medarda' (a site that could not be re-located for the present review), Villasana, and Yacaré. The following collections are in the USNTC: RML

056842 (one female, host unknown, Puerto Max, 9 March 1905, coll. L. des Arts), RML 088290 (two females, host unknown, Puerto Max, date unknown, coll. A. Vezenji), RML 105913 (three nymphs, ex Mazama sp., Colonia Mennonita SW, 8 July 1977, coll. T. W. Nelson), RML 105915 (five nymphs, ex Mazama sp., Transchaco Road km 580-620, 25 July 1977, coll. T. W. Nelson), RML 105916 (four nymphs, ex Mazama sp., Transchaco Road km 580-620, 18 July 1977, coll. T. W. Nelson), RML 105917 (15 nymphs, ex Tayassu sp., Transchaco Road km 580-620, 30 July 1977, coll. T. W. Nelson), RML105918 (six nymphs, ex Mazama sp., Transchaco Road km 580-620, 8 August 1977, coll. T. W. Nelson), RML 117977 (one female, host unknown, Parque Defensores del Chaco, 5 December 1981, coll. J. A. Kochalka), RML 119014 (two males and one female, ex Catagonus wagneri, Chaco Boreal, January 1982, coll. 'staff of Museum A. Koenig, Bonn'), RML 119162 (two males and two females, ex Ca. wagneri, Toledo, 1988, coll. K. Benirschke), RML 119709 (one male, ex Ca. wagneri, locality and date unknown, coll. K. Benirschke), RML 123654 (two females, ex Puma concolor, Estancia Faro Moro, 22 June 2002, coll. M. Cunningham), RML 123661 (one female, ex Pa. onca, Parque Defensores del Chaco, 16 July 2003, coll. M. Cunningham), RML 123662 (one male, ex Pa. onca, Parque Defensores del Chaco, 18 July 2003, coll. M. Cunningham), and RML 123666 (one female, ex Pu. concolor, Estancia Faro Moro, July 2004, coll. M. Cunningham). The TCDE also contains some specimens of Am. cajennense: GR039 (two males, three females and 10 nymphs, Villarica, host, date and collector unknown), GR041 (one female, ex human, Villarica, 12 February 1947, collector unknown) and GR044 (one female, ex human, Villarica, October 1945, collector unknown). Although Ciudad del Este is in the PaPP, all the other localities are in the ChPP. Amblyomma cajennense is a commonly encountered tick

from northern Argentina northward throughout the Neotropics to the southern U.S.A. (Nearctic).

Amblyomma calcaratum Neumann. Neumann (1899) recorded Am. calcaratum from Paraguay, but without host or locality data. This species is known from Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Surinam, Trinidad and Tobago, and Venezuela, where it is a common parasite of the giant anteater (Myrmecophaga tridactyla) and collared anteater (Tamandua tetradactyla).

Amblyomma coelebs Neumann. Keirans (1985) reported this species from San Pedro, although it is not clear whether the specimens were removed from a dog, human or cow or from vegetation. The TCDE contains just one accession: GR043 (one male and two females, ex human, Villarica, October 1945, coll. unknown). Both known collection sites are in the ChPP. Adults of Am. coelebs are chiefly found on Perissodactyla, in most countries from northern Argentina to Mexico.

Amblyomma dissimile Koch. Dios and Knopoff (1930) identified this tick from snakes (Lachesis sp.) in Asunción, whereas Massi Pallarés and Benítez Usher (1982) reported it from both Asunción and Villarica, on reptiles and amphibians. These localities all lie within the ChPP. Amblyomma dissimile is a common parasite of reptiles and true toads of the genus Bufo, from Argentina northward to southern Mexico, the Caribbean islands and the southern Nearctic (Florida).

Amblyomma dubitatum Neumann. Robinson (1926) reported this species (as Am. cooperi) from Puerto Cooper, whereas Massi Pallarés and Benítez Usher (1982) recorded it (again as Am. cooperi) on capybara (Hydrochaeris hydrochaeris) from San Juan Bautista, Estancia San Rafael and Santa Medarda. The USNTC (RML 034690) contains just

one male and one female, collected from *H. hydrochaeris* at 'Rio South of Descalvadez' (another site that could not be re-located for the present review), date and collector unknown. All confirmed localities for Paraguayan *Am. dubitatum* are situated in the ChPP. This tick has also been found on capybara in Argentina, Bolivia, Brazil and Uruguay.

Amblyomma incisum Neumann. The USNTC (RML 056844) contains a female tick identified as 'probably Am. incisum' but without additional data. Under accession GR047, the TCDE has a female identified as this species (ex human, Villarica, October 1945, collector unknown) which comes from within the ChPP. Labruna et al. (2005) showed, however, that, on several occasions, Am. incisum has been confused with Amblyomma latepunctatum Tonelli-Rondelli or Amblyomma scalpturatum Neumann. The known range of Am. incisum includes Argentina, Bolivia, Brazil and Peru; its presence in Ecuador, French Guiana, Guyana, and Venezuela is uncertain. Tapirus terrestris is this species' principal host.

Amblyomma longirostre (Koch). Although Massi Pallarés and Benítez Usher (1982) reported this tick from Sphiggurus villosus in Caaguazú (PaPP), Wilson and Reeder (1993) state that this host only occurs in Brazil. Adults of Am. longirostre have also been collected in Argentina, Bolivia, Brazil, French Colombia, Guiana, Mexico, Trinidad Panama, and Tobago, Venezuela. Nymphs infest birds that disperse beyond the range of the porcupines, of the genera Coendou and Sphiggurus, that are the principal hosts of the adult ticks.

Amblyomma nodosum Koch. Massi Pallarés and Benítez Usher (1982) reported a collection of Am. nodosum from an unidentified anteater in Garay Cué (ChPP). This tick species shares hosts with Am. calcaratum, and differentiating the two tick species is not

always easy. Amblyomma nodosum has also been found in Argentina, Bolivia, Brazil, Colombia, Costa Rica, Guatemala, Mexico, Nicaragua, Panama, Trinidad and Tobago, and Venezuela.

Amblyomma ovale Koch. Berlese (1888) first reported this species (as Am. auronitens) from Paraguay, on the basis of unattached collected Río specimens at Apa. Subsequently, this tick has been collected several times, from a variety of carnivores or from humans, in Coronel Oviedo, Asunción, Luque, Puerto Cooper, Villa de San Pedro, Villarica, Yacaré, San Pedro, Estancia San Rafael and Rancho Alegre localities that are all within the ChPP (Massi Pallarés and Benítez Usher, 1982; Keirans, 1985; Guglielmone et al., 2003c). The USNTC contains RML 088296 female, host unknown, Asunción, 1900, coll. D. Anisitis), and RML 088297 (two males and two females, ex dog, Asunción, 14 October 1904, coll. A. Vezenji). The TCDE holds GR033 (one male, 1931, no further data), GR037 (two males and two females, ex dog, Villarica, 14 September 1946, coll. unknown), and GR041 (one male, ex human, Villarica, 9 Februrary 1947, coll. unknown). Amblyomma ovale ranges from north-central Argentina northward throughout the Neotropical Region to Nearctic Mexico; there are also a few records from the U.S.A. (Guglielmone et al., 2003c).

Amblyomma pacae Aragão. Robinson (1911) reported a collection of Am. pacae from an unknown host in San Bernardino (ChPP). The range of this tick, which commonly infests Agouti paca, also encompasses Belize, Brazil, Colombia, Guyana, Panama, Surinam and Venezuela.

Amblyomma parvum Aragão. An infestation with Am. parvum of cattle in Filadelfia was described by Quinlan et al. (1980), while Whitaker and Abrell (1987) found this tick on the carnivores Cerdocyon thous and Nasua

nasua as well as the armadillo Tolypeutes mataco (localities unknown). The following Paraguayan collections are in the USNTC: RML 118132 (one female, ex Ca. wagneri, Filadelfia, 18 September 1985, coll. K. Benirschke), RML 119161 (one female, ex wagneri, Toledo, 1988, coll. K. Benirschke), and RML 119709 females, ex Ca. wagneri, Toledo, 1988, coll. K. Benirschke). Also in the USNTC are many, more recent collections of adult Am. parvum from carnivores in Paraguay, all collected by M. Cunningham — RML 123653 (27 males and two females, ex Pu. concolor, 22 June 2002), RML 123654 (two males and two females, ex Pu. concolor, 22 June 2002), RML 123655 (one male and two females, ex Pu. concolor, 26 June 2002), RML 123656 (two males, ex Pu. concolor, 3 June 2002), RML 123657 (one male and two females, ex Pu. concolor, 4 July 2003), RML 123658 (one male and four females, ex Pu. concolor, 17 June 2002) and RML 123659 (three males and one female, ex Pa. onca, 21 June 2002) all came from Boquerón, Estancia Faro Moro, whereas RML 123660 (one male, ex Pa. onca, 3 June 2002) came from Filadelfia, RML 123663 (four males, ex Oncifelis geoffroyi, 16 June 2002), RML 123665 (one male, ex 'fox', 22 June 2002) and RML 123666 (one female, ex Pu. concolor, July 2004) from Estancia Faro Moro, and RML 123667 (one male and four females, ex Pa. onca, 26 June 2004) and RML 123668 (three males and seven females, ex Pa. onca, 27 2004) from Parque Nacional Defensores del Chaco. All known collection sites for Paraguayan Am. parvum lie in the ChPP. This tick, which infests a variety of hosts, is also known from Argentina, Bolivia, Brazil, Costa Rica, El Salvador, French Guiana, Mexico, Nicaragua, Panama and Venezuela.

Amblyomma pseudoconcolor Aragão. Robinson (1926) reported a collection of this species from an unknown host in San Bernardino (ChPP), while Whitaker and Abrell (1987) found it on *Chaetophractus villosus* and *E. sexcinctus*, without providing locality data. The USNTC contains two accessions, both from the ChPP: RML 105927 (one male, three nymphs and five larvae, ex *Tolypeutes* sp., Cerro León, 11 July 1977, coll. K. Colin) and RML 122225 (one male, ex *To. mataco*, Toledo, 30 November 1995, coll. M. Campbell). *Amblyomma pseudoconcolor* is common on armadillos and has been found in Argentina, Bolivia, Brazil, French Guiana, Surinam and Uruguay.

Amblyomma rotundatum Koch. Although there have been no published reports of this reptile and amphibian ectoparasite from Paraguay, the USNTC contains Paraguayan collections labelled Am. rotundatum: four taken, by an unknown collector, from Bufo marinus in Asunción, September 1926 — RML 032213 (one nymph), RML 032214 (one female), RML 032219 (one female) and RML 032217 (one nymph and three larvae; labelled 'A. rotundatum probable') — and two taken, by an unknown collector, on an unknown date and at an unspecified site, from Bu. marinus — RML 032216 (one female and one nymph) and RML 032218 (one female and one nymph). Asunción is located in the ChPP. Amblyomma rotundatum ranges from Argentina northward to the Nearctic Region (Florida) and the Caribbean islands.

Amblyomma scutatum Neumann. Neumann (1899) reported nymphs of Am. scutatum from a Paraguayan bat (Noctilio albiventris) but provided no locality data. There are no additional Paraguayan records of Am. scutatum, which is an ectoparasite of reptiles in Brazil, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua and Venezuela.

Amblyomma tigrinum Koch. Massi Pallarés and Benítez Usher (1982) reported adults and immature stages of this tick from several

mammals and birds in Colonia Neuland, Estancia Campo-í, Toledo, Asunción, Villeta, Río Apa, San Bernardino, General Artigas, San Juan Bautista, San Fernando, Yacaré, Estancia Barrerito, Paraguarí, Rancho Quindy, Alegre, and Santa Medarda. The USNTC contains the following adult specimens of Am. tigrinum from Paraguay: RML 123657 (one female, ex Pu. concolor, Estancia Faro Moro, 4 July 2003, coll. M. Cunningham), RML 123659 (three females, ex Pa. onca, Estancia Faro Moro, 21 June 2002, coll. M. Cunningham), and RML 123660 (one male and three females, ex Pa. onca, Filadelfia, 3 June 2002, coll. M. Cunningham). The TCDE contains a single male (GR017) collected from a human (no further data). General Artigas is situated in the PaPP but all the other confirmed localities lie within the ChPP. Adults of Am. tigrinum are common parasites of wild and domestic Canidae (Guglielmone et al., 2000). Although birds appear to be the principal hosts of the larvae and nymphs (González Acuña et al., 2004), Caviidae and sigmodontine rodents in Argentina are commonly found infested with the immature stages of this tick (Nava et al., 2006). This is a South American tick, with confirmed records for Argentina, Bolivia, Brazil, Chile, French Guiana, Peru, Uruguay and Venezuela (Estrada-Peña et al., 2005). Amblyomma tigrinum was long confused with Am. maculatum until these two taxa were differentiated by Kohls (1956).

Amblyomma triste Koch. The Paraguayan collections of this species are in the USNTC: RML 056301 (one male and one female, ex tapir, locality unknown, 1917, coll. E. Joukowsky). The other Paraguayan specimens of Am. triste in the USNTC, all collected in Estancia Faro Moro by M. Cunningham, are RML 123657 (one male, ex Pu. concolor, 4 July 2003) and RML 123659 (three males, ex Pa. onca, 21 June 2002). Amblyomma triste has been found, on a variety of hosts, in Argentina, Brazil, Colombia, Ecuador,

Peru, Uruguay and Venezuela (Estrada-Peña et al., 2005).

Dermacentor Koch; Dermacentor nitens Neumann. This tick has been found on horses in Coronel Oviedo, Mbocayaty, Villarica, Maldonado Cué, Villasana and Paraguarí, and on cattle in Estancia Surubíy (Quinlan et al., 1980; Massi Pallarés and Benítez Usher, 1982). A recent collection (INTA 1920) was of four males, seven females and one nymph from a horse in San Pedro (19 June 2005, coll. C. Rebollo). All of the known collection sites lie in the ChPP. Dermacentor nitens is common on horses from northern Argentina northward through the Neotropics, including the Caribbean islands, and, occasionally, into the Nearctic Region (Florida).

Haemaphysalis Koch; Haemaphysalis juxtakochi Cooley. Massi Pallarés and Benítez Usher (1982) reported this species on deer, hare and wild pig in San Fernando, Yacaré and Rancho Alegre. There are two Paraguayan collections of Ha. juxtakochi in the USNTC, both collected by R. L. Martin: RML 064767 (six nymphs, ex Sylvilagus brasiliensis, Fortín Juan de Zalazar, 20 September 1973) and RML 064768 (two nymphs and one larva, ex S. brasiliensis, Río Pirapó area, 12 July 1974). These records indicate that Ha. juxtakochi occurs in both the PaPP and ChPP. Adults of this species are usually found on Artiodactyla, especially deer of the genus Mazama, in most countries of South and Central America; there are also a number of records from the Nearctic Region.

Haemaphysalis leporispalustris (Packard). Nuttall and Warburton (1915) reported Ha. leporispalustris from an unknown host in San Bernardino. There is a single USNTC accession: RML 031688 (one male, ex Dasyprocta azarae, Yhu Sommerfield village, 8 March 1959, coll. M. Hertig). These localities represent both the PaPP

and ChPP. Adults infest Lagomorpha in the Neotropical Region (Argentina, Bolivia, Brazil, Colombia, Costa Rica, Guatemala, Panama, Paraguay, Peru and Venezuela) and Nearctic.

Ixodes Latreille; Ixodes loricatus Neumann. Massi Pallarés and Benítez Usher (1982) collected I. loricatus on marsupials in Puerto Cooper and Sapucai (both in the ChPP), and Keirans (1982) recorded it, albeit only as 'probable' I. loricatus, from Didelphis sp. in Sapucai. As Massi Pallarés and Benítez Usher (1982) stated that I. loricatus is prevalent in eastern Paraguay, this tick may also occur in the Amazonic domain. Adults of I. loricatus are specific to American marsupials, in Argentina, Brazil, Guatemala, Mexico, Paraguay, Uruguay and Venezuela.

Rhipicephalus Koch; Rhipicephalus microplus (Canestrini). This tick is a wide-spread parasite of cattle in the Afrotropical, Australian, Neotropical and Oriental zoogeographical regions. Massi Pallarés and Benítez Usher (1982) stated that, although Rh. microplus is most common in the Oriental Region, it is widely found on cattle in Paraguay; it is therefore probably established throughout the Amazonic and Chaco domains. Paraguay is, in fact, the type locality of Rh. microplus, which was described by Canestrini (1887), as Haemaphysalis micropla. It has been collected from cattle in Estancia Villa Ana and Río Apa, Estancia Barrerito, Estancia Naranja-y, Chaco Experimental Station and Filadelfia, and has been found on cattle and horses in Villarica and on tapir in Colonia Risso (Berlese, 1888; Tonelli Rondelli, 1931; Minning, 1934; Quinlan et al., 1980; Brizuela et al., 1996). Berlese (1888) and Minning (1934) proposed the names Haemaphysalis micropla and Uroboophilus microplus for this species, respectively. There is only a single Paraguayan collection of Rh. microplus in the USNTC [RML 072607 (one female, host unknown, Puerto Max, January 1957,

coll. A. Vezenyi)] and only one in the TCDE [GR056 (one female, ex Mazama sp., Villarica, November 1945, collector unknown)]. There are, however, several more recent collections at INTA, all taken from cattle by C. Rebollo: INTA 1917 (19 females, Guarambaré, 10 July 2005), INTA 1918 (one male and 20 females, Villarica, 10 June 2005), INTA 1921 (seven males, 19 females and two nymphs, San Pedro, 19 June 2005), INTA 1927 (four males, 16 females and one nymph, Sapucai, 10 June 2005), INTA 1931 (eight females, San Juan Bautista, 10 March 2005) and INTA 1934 (one male and five females, San Ignacio, 6 February 2005).

Rhipicephalus sanguineus (Latreille). This species was reported by Massi Pallarés and Benítez Usher (1982) on dogs in Asunción, Paraguarí and San Fernando. Recent collections, all taken from dogs by C. Rebollo, are stored at INTA, as INTA 1919 (one male and 16 females, Asunción, 10 June 2005), INTA 1925 (three males and three females, San Lorenzo, 8 July 2005) and INTA 1926 (six males and 12 females, Ciudad del Este, 10 June 2005). All but one of the known localities lie within the ChPP; Ciudad del Este is in the PaPP. Rhipicephalus sanguineus is an African tick that has spread throughout the world, with humans and their dogs.

Tick Species Probably Endemic or Established in Paraguay

ARGASIDAE Canestrini

Argas miniatus Koch. This species is a common parasite of chickens in Neotropical countries. Many reports of Ar. persicus, a Palearctic species, on poultry in the Neotropics may actually represent misidentifications of Ar. miniatus or another related species (Kohls et al., 1970). Although Paraguayan specimens indistinguishable from Ar. persicus were examined by Kohls et al. (1970), and Aragão (1936) mentions the presence of Ar. persicus on domestic birds (at unspecified localities) in

Paraguay, it remains possible that Ar. miniatus is also present in this country's chicken houses.

Argas monachus Keirans, Radovsky and Clifford. This tick has only been found in Argentina (Guglielmone et al., 2003a), where it is known from Formosa, a province that borders Paraguay (Ivancovich and Luciani, 1992). As this species' known host, the parakeet Myiopsitta monachus can be found in Paraguay, it seems likely that Ar. monachus also occurs in the country.

IXODIDAE Murray

Amblyomma argentinae Neumann. To date, this tick has only been found in Argentina, where it is a common ectoparasite of the land tortoise *Chelonoidis chilensis* (Guglielmone et al., 2001). Since the range of this tortoise includes western Paraguay (Cei, 1993), it seems likely that *Ar. argentinae* also occurs there.

Amblyomma humerale Koch. This is a reptile tick that has been found on *Geochelone denticulata* in the Bolivian department of Santa Cruz, which is contiguous with northern Paraguay (Robbins *et al.*, 2003). The range of *Am. humerale*, which covers parts of Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Surinam, Peru, Trinidad and Tobago, and Venezuela, may therefore also include Paraguay.

Amblyomma naponense (Packard). This species is common on peccaries (Tayassu and *Pecari* spp.), and there are records of its occurrence in areas close to Paraguay: the department of Bolivian Santa Cruz (Robbins et al., 1998) and the Brazilian state of Mato Grosso do Sul (Guimaraes et al., 2001). This tick has been found in Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Peru, Surinam and Venezuela, and it seems likely that its range also includes parts of Paraguay.

Amblyomma oblongoguttatum Koch. This tick has been found on a variety of hosts in

several South and Central American countries. It is known from the department of Santa Cruz in Bolivia (Robbins *et al.*, 1998) and the state of Paraná in Brazil (Ribeiro, 1966) — areas immediately to the north and east of Paraguay, respectively. It is highly likely that *Am. oblongoguttatum* occurs throughout a large part of Paraguay.

Amblyomma pseudoparvum Guglielmone, Mangold and Keirans. The principal host of Am. pseudoparvum appears to be the caviid Dolichotis salinicola. Both tick and host have been found in the Argentinian province of Salta, which shares a short border with Paraguay (Guglielmone et al., 1990), where Do. salinicola also occurs (Wilson and Reeder, 1993).

Ixodes aragaoi Fonseca OR Ixodes pararicinus Keirans and Clifford. These two species are morphologically similar, and it is still unclear whether they represent distinct taxa (Guglielmone et al., 2003a); both have also long been confused with the Palearctic Ixodes ricinus Linnaeus. Ixodes pararicinus has been found on cattle in the Argentinean province of Formosa, which borders southwestern Paraguay (Ivancovich and Luciani, 1992), whereas I. aragaoi has been found on an undetermined species of deer in the Brazilian state of Paraná, which borders eastern Paraguay (Ribeiro, 1966).

Ixodes auritulus Neumann. This tick, a parasite of birds from southern Argentina to Canada in the Americas, is known from the Brazilian state of Paraná, which is contiguous with eastern Paraguay (González-Acuña et al., 2005). Given the relative ease with which its hosts can traverse long distances, I. auritulus should be expected to occur in Paraguay.

Ixodes luciae Sénevet. Adults of this tick infest marsupials from Argentina to southern Mexico. Fonseca (1959) found *I. luciae* close to northern Paraguay, in the Bolivian state of Santa Cruz.

Tick Species Erroneously Reported from Paraguay

Argasidae Canestrini

Ornithodoros coriaceus Koch. This argasid is found in the Nearctic Region and also in the Neotropical portion of southern Mexico. Its supposed presence in Paraguay (Río Apa) was cited by Berlese (1888), but Tonelli Rondelli (1939) examined the nymphal specimen that was the basis for this record and found it to be an undeterminable *Ornithodoros* that was different from *Orn. coriaceus*.

IXODIDAE Murray

Amblyomma americanum (Linnaeus). This is a strictly Nearctic species. Although, according to Casanueva (2001), Bishopp and Trembley (1945) reported the presence of Am. americanum in Paraguay, these authors did not, in fact, include Paraguay in their discussion of this species' range.

Amblyomma maculatum Koch. Neumann (1899) reported males, females and nymphs of Am. maculatum from an unknown host and locality in Paraguay. Prior to the resurrection of Am. tigrinum and Am. triste by Kohls (1956), these species were often mis-identified as Am. maculatum, which does not occur in southern South America. Amblyomma maculatum is a Neotropical-Nearctic species, with bona fide records only Colombia, Costa from Belize, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Peru, the U.S.A. and Venezuela (Estrada-Peña et al., 2005).

DISCUSSION

The Paraguayan tick fauna is currently known to consist of 30 species but it seems likely that several other species may be present. To date, most tick records have been from the Chaco, rather than Amazonic, domain, and no specimens from Paraguay's relatively small CePP were available for the present review. Nonetheless, the present study yielded three new records for Paraguay: *Orn. hasei, Am. rotundatum* and *Am. triste.* As expected,

collection frequency was largely a function of human-population density, most collections having been made in the populous centre of the country, especially in the area around metropolitan Asunción.

The brown dog tick, Rh. sanguineus, is the most widely distributed tick species in the world (Keirans, 1992) and is able to complete its life-cycle indoors (Koch, 1982). This species has, surprisingly, only been recorded in a few localities in the ChPP and PaPP, and it is almost certainly much more wide-spread in Paraguay than these records indicate. As Oliveira et al. (2005) and Szabó et al. (2005) recently found morphological, biological and molecular evidence to support the presence of two species of the Rh. sanguineus tick group in Argentina and Brazil, additional studies of Paraguayan 'Rh. sanguineus' are needed, to determine whether these ticks represent Rh. sanguineus sensu stricto, a closely related taxon, or both.

Amblyomma tigrinum was found in both the Amazonic and Chaco domains, which accords with Guglielmone et al. (2000), who observed that this species is able to colonize regions with vastly different climates, including the xeric environment of Patagonia, in southernmost Argentina. The Paraguayan ranges of Am. parvum and Am. cajennense appear to be extensions of their ranges in Argentina, with Am. parvum restricted to dry areas of the Chaco domain and Am. cajennense more widespread, even in the Amazonic domain (Mangold et al., 1990; Guglielmone et al., 1990). In contrast, Am. aureolatum, which has only been recorded at one site in Paraguay, appears to be less abundant and significantly more restricted in distribution than the related Am. ovale. Additional research is needed to understand the distribution of both of these species, although it appears that, in general, the range of Am. ovale is more extensive than that of Am. aureolatum in the central and western portions of the Neotropical Region (Guglielmone et al., 2003c). Paraguay would benefit from a country-wide survey of its ticks, to delimit precisely the ranges of those tick species that are of medical or veterinary

importance or that are key indicators of biodiversity.

The reptile and amphibian parasites Am. dissimile and Am. rotundatum are known to produce long-lasting wounds; they may also affect the reticulo-endothelial system of their hosts and transmit toxins (Aragão, 1936; Jakowska, 1972). Rhipicephalus microplus and Rh. sanguineus are well known for their capacity to heavily infest cattle and dogs, respectively, and to transmit disease-causing pathogens to their hosts (Guglielmone, 1995; Bool and Sutmöller, 1957). The same applies to infestations of horses with De. nitens (Friedhoff and Soulé, 1996) and of chickens with Ar. persicus or Ar. miniatus (Hoogstraal, 1985). Argas miniatus may cause paralysis in its avian hosts (Magalhães et al., 1987). collections Additional of argasids Paraguay are needed in order to confirm the presence of Ar. miniatus and resolve the issue of whether Ar. persicus and/or a sibling species occurs in the country's chicken houses. Recently, Petney et al. (2004) used molecular evidence to verify the presence of Ar. persicus sensu stricto in Australia; similar studies are needed to determine the taxonomic status of specimens hitherto identified as Ar. persicus in Paraguay and other Neotropical countries.

It is important to note that Orn. rudis, Am. aureolatum, Am. brasiliense, Am. cajennense, Am. coelebs, Am. incisum, Am. ovale and Am. tigrinum have all been found on humans in Paraguay. Moreover, Massi Pallarés and Benítez Usher (1982) suspect that *Orn. rostratus* also attacks humans in Paraguay, as it does in Argentina (Boero, 1957). Ambylomma parvum and Am. triste appear to be frequent ectoparasites of humans in Argentina and Uruguay, respectively (Guglielmone et al., 1991; Venzal et al., 2003), and probably therefore also attack humans in Paraguay. Ornithodoros talaje/Orn. puertoricensis, Am. calcaratum, Am. dissimile, Am. dubitatum, Am. longirostre, Am. pacae, Am. pseudoparvum, Am. rotundatum, De. nitens, Ha. juxtakochi, Ha. leporispalustris, Rh. microplus and Rh. sanguineus have all been found attached to humans in several Neotropical countries (Guglielmone et al., 2003a).

Although there appear to be no published reports of ticks transmitting pathogens to humans in Paraguay, both Am. cajennense and Am. triste are known to transmit rickettsiae (Rickettsia rickettsii and Ri. parkeri, respectively) in other South American countries (Labruna, 2004; Venzal et al., 2004), and Ri. rickettsii has been isolated from Am. aureolatum (Salles Gomes, 1933). Ornithodoros rostratus, Orn. rudis, Ha. leporispalustris and Rh. sanguineus may play a role in the maintenance of rickettsiae of the spottedfever group (Hoogstraal, 1985; Labruna, 2004). Bites of Orn. rostratus are extremely painful to humans, causing itching, inflammation and blisters (Boero, 1957), and members of the genus Ornithodorus are involved in the transmission of relapsing fever spirochaetes in South America (Hoogstraal, 1985). Ehrlichia canis or a closely related species has been isolated from humans in Venezuela (Perez et al., 1996), and evidence indicates that Rh. sanguineus is the vector (Unver et al., 2001). These observations indicate that, apart from their veterinary impact, a significant number of Paraguayan ticks may pose a threat to human health.

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REFERENCES

- Adámoli, J. (1985). Ecología del Chaco Paraguayo. Revista Forestal, 6, 1–19.
- Aragão, H. B. (1936). Ixodidas brasileiros e de algunos paízes limitrophes. *Memórias do Instituto Oswaldo Cruz*, 31, 759–843.
- Barker, S. C. & Murrell, A. (2002). Phylogeny, evolution and historical zoogeography of ticks: a review of recent progress. Experimental and Applied Acarology, 28, 55–68.
- Berlese, A. (1888). Acari Austro-Americani. *Bolletino della Società Entomologica Italiana*, **20**, 171–242.

- Bishopp, F. & Trembley, H. L. (1945). Distribution and hosts of certain North American ticks. *Journal of Parasitology*, 31, 1–54.
- Boero, J. J. (1957). Las Garrapatas de la República Argentina (Acarina: Ixodoidea). Buenos Aires: Departamento Editorial, Universidad de Buenos Aires.
- Bool, P. H. & Sutmöller, P. (1957). Ehrlichia canis infection in dogs on Aruba (Netherlands Antilles). Journal of the American Veterinary Medical Association, 130, 418–420.
- Brizuela, C. M., Ortellado, C. A., Sanchez, T. I., Osorio, O. & Walker, A. R. (1996). Formulation of integrated control of *Boophilus microplus* in Paraguay: analysis of natural infestations. *Veterinary Parasitology*, 63, 95–108.
- Cabrera, A. L. & Willink, A. (1973). Biogeografia de América Latina. Monografias No. 13 Serie de Biología. Washington, DC: Organización de los Estados Americanos.
- Canestrini, G. (1887). Intorno ad alcuni Acari ed Opilonidi dell'America. Atti della Società Veneto-Trentina di Scienze Naturali Residenti in Padova, 11, 100–109.
- Capriles, J. M. & Gaud, S. M. (1977). The ticks of Puerto Rico (Arachnida: Acarina). Journal of Agriculture of the University of Puerto Rico, 61, 402–404.
- Casanueva, M. E. (2001). Muscular system of the Amblyomma americanum larvae (Acari: Ixodidae). Revista Chilena de Anatomía, 19, 285–290.
- Cei, J. M. (1993). Reptiles del Noroeste, Nordeste y Este de la Argentina. Herpetofauna de las Selvas Subtropicales, Puna y Pampas. Monografie No. 14. Torino, Italy: Museo Regionale di Scienze Naturali.
- Cordero, E. H., Vogelsang, E. G. & Cossio, V. (1928). Ornithodoros talaje (Guérin-Méneville) y su presencia en el Paraguay y en el Uruguay. Physis, 9, 125–127.
- Dios, R. L. & Knopoff, R. (1930). Sobre Ixodoidea de la República Argentina. Revista de la Sociedad Argentina de Biología, 6, 593-627.
- Estrada-Peña, A., Venzal, J. M., Mangold, A. J., Cafrune, M. M. & Guglielmone, A. A. (2005). The *Amblyomma maculatum* Koch, 1844 (Acari: Ixodidae: Amblyomminae) tick group: diagnostic characters, description of the larva of *A. parvitarsum* Neumann, 1901, 16S rDNA sequences, distribution and hosts. *Systematic Parasitology*, **60**, 99–112.
- Fonseca, F. (1959). Notas de acarología. XLIVI. Acarofauna zooparasita na Bolivia. Memórias do Instituto Butantan, 29, 89–141.
- Friedhoff, K. T. & Soulé, C. (1996). An account of equine babesioses. *Revue Scientifique et Technique Office International des Epizooties*, **15**, 1191–1201.
- González Acuña, D. & Guglielmone, A. A. (2005). The ticks (Acari: Ixodoidea: Argasidae: Ixodidae) of Chile. Experimental and Applied Acarology, 35, 147–163.
- González-Acuña, D., Venzal, J., Skewes-Ramm, O.,
 Rubilar-Contreras, L., Daugschies, A. &
 Guglielmone, A. A. (2004). First records of immature stages of Amblyomma tigrinum (Acari: Ixodidae)

- on wild birds in Chile. Experimental and Applied Acarology, 33, 153-156.
- González-Acuña, D., Venzal, J. M., Keirans, J. E., Robbins, R. G., Ippi, S. & Guglielmone, A. A. (2005). New host and locality records for the *Ixodes auritulus* Neumann, 1904 (Acari: Ixodidae) species group, with a review of host relationships and distribution in the Neotropical Zoogeographic Region. *Experimental and Applied Acarology*, 37, 147–156.
- Guglielmone, A. A. (1995). Epidemiology of babesiosis and anaplasmosis in South and Central America. Veterinary Parasitology, 57, 109–119.
- Guglielmone, A. A., Mangold, A. J. & Keirans, J. E. (1990). Redescription of the male and female of Amblyomma parvum Aragao, 1908, and description of the nymph and larva, and description of all stages of Amblyomma pseudoparvum sp.n. (Acari: Ixodida: Ixodidae). Acarologia, 31, 144–159.
- Guglielmone, A. A., Mangold, A. J. & Viñabal, A. E. (1991). Ticks (Ixodidae) parasitizing humans in four provinces of northwestern Argentina. *Annals of Tropical Medicine and Parasitology*, 85, 539–542.
- Guglielmone, A. A., Mangold, A. J., Luciani, C. A. & Viñabal, A. E. (2000). Amblyomma tigrinum (Acari: Ixodidae) in relation to phytogeography of centralnorthern Argentina with note on hosts and seasonal distribution. Experimental and Applied Acarology, 24, 983–989.
- Guglielmone, A. A, Luciani, C. A. & Mangold, A. J. (2001). Aspects of the ecology of Amblyomma argentinae Neumann, 1904 [= Amblyomma testudinis (Conil, 1877)] (Acari: Ixodidae). Systematic and Applied Acarology Special Publications, 8, 1–12.
- Guglielmone, A. A., Estrada-Peña, A., Keirans, J. E. & Robbins, R. G. (2003a). Ticks (Acari: Ixodida) of the Neotropical Zoogeographic Region. Houten, The Netherlands: Atalanta.
- Guglielmone, A. A., Estrada-Peña, A., Luciani, C. A., Mangold, A. J. & Keirans, J. E. (2003b). Hosts and distribution of Amblyomma auricularium (Conil, 1878) and Amblyomma pseudoconcolor Aragão, 1908 (Acari: Ixodidae). Experimental and Applied Acarology, 29, 131–139.
- Guglielmone, A. A., Estrada-Peña, A., Mangold, A. J., Barros-Battesti, D. M., Labruna, M. B., Martins, J. R., Venzal, J. M., Arzua, M. & Keirans, J. E. (2003c). Amblyomma aureolatum (Pallas, 1772) and Amblyomma ovale Koch, 1844 (Acari: Ixodidae): hosts, distribution and 16S rDNA sequences. Veterinary Parasitology, 113, 273–288.
- Guglielmone, A. A., Mangold, A. J. & Estrada-Peña, A. (2005). Are Antricola species proper representatives of the genus Carios? Newsletter on Ticks and Tick-borne Diseases of Livestock in the Tropics, 27, 42–43.
- Guimaraes, J. H., Tucci, E. D. & Barros Battesti, D. M. (2001). Ectoparasitos de Importancia Veterinaria. São Paulo, Brazil: Pleiade–FAPESP.

- Hoogstraal, H. (1985). Argasid and nuttalliellid ticks as parasites and vectors. Advances in Parasitology, 24, 135–238.
- Ivancovich, J. C. & Luciani, C. A. (1992). Las Garrapatas de Argentina. Buenos Aires: Asociación Argentina de Parasitología Veterinaria.
- Jakowska, S. (1972). Lesions produced by ticks, Amblyomma dissimile, in Bufo marinus toads from the Dominican Republic. American Zoologist, 12, 731.
- Jones, E. K., Clifford, C. M., Keirans, J. E. & Kohls, G.M. (1972). The ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of Amblyomma in the Western Hemisphere. Brigham Young University Science Bulletin, Biological Series, 17, 1–40.
- Keirans, J. E. (1982). The tick collection (Acarina: Ixodoidea) of the Hon. Nathaniel Charles Rothschild deposited in the Nuttall and general collections of the British Museum (Natural History). Bulletin of the British Museum (Natural History), Zoology Series, 42, 1–36.
- Keirans, J. E. (1985). George Henry Falkiner Nuttall and the Nuttall Tick Catalogue. Agricultural Research Service Miscellaneous Publications No. 1438. Washington, DC: United States Department of Agriculture.
- Keirans, J. E. (1992). Systematics of the Ixodida (Argasidae, Ixodidae, Nuttalliellidae): an overview and some problems. In *Tick Vector Biology, Medical* and Veterinary Aspects, eds Fivaz, B., Petney, T. & Horak, I. pp. 1–21. Berlin: Springer.
- Klompen, J. S. H. & Oliver, J. H. (1993). Systematic relationship in the soft ticks (Acari: Ixodida: Argasidae). Systematic Entomology, 18, 313–331.
- Koch, H. G. (1982). Oviposition of the brown dog tick (Acari: Ixodidae) in the laboratory. *Annals of the Entomological Society of America*, 75, 583–586.
- Kohls, G. M. (1956). Concerning the identity of Amblyomma maculatum, A. tigrinum, A. triste, and A. ovatum of Koch, 1844. Proceedings of the Entomological Society of Washington, 58, 143–147.
- Kohls, G. M., Sonenshine, D. E. & Clifford, C. M. (1965). The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). II. Identification of the larvae of the Western Hemisphere and description of three new species. *Annals of the Entomological Society of America*, 58, 331–364.
- Kohls, G. M., Hoogstraal, H., Clifford, C. M. & Kaiser, M. N. (1970). The subgenus *Persicargas* (Ixodoidea, Argasidae, *Argas*). 9. Redescription and New World records of *Argas* (*P.*) *persicus* (Oken), and resurrection, redescription and records of *A.* (*P.*) *sanchezi* Dugès and *A.* (*P.*) *miniatus* Koch, New World ticks misidentified as *A.* (*P.*) *persicus. Annals of the Entomological Society of America*, **63**, 590–606.
- Labruna, M. B. (2004). Carta acarológica. Revista Brasileira de Parasitologia Veterinária, 13 (Suppl. 1), 199–202.
- Labruna, M. B., Keirans, J. E., Camargo, L. M. A., Ribeiro, A. F., Martins, R. S. & Camargo, E. P. (2005). Amblyomma latepunctatum, a valid tick species (Acari. Ixodidae) long misidentified with

- Amblyomma incisum and Amblyomma scalpturatum. Journal of Parasitology, **91**, 527–541.
- Magalhães, F. E. P., Massard, C. L. & Serra Freire, N. M. (1987). Paralysis in Gallus gallus and Cairina moschata induced by larvae of Argas (Persicargas) miniatus. Pesquisa Veterinária Brasileira, 7, 47–49.
- Mangold, A. J., Gualberto, A. & Guglielmone, A. A. (1990). La distribución geográfica de *Amblyomma cajemense* Fabricius, 1787 (Acari: Ixodoidea: Ixodidae) en Argentina. *Veterinaria Argentina*, 7, 306–315.
- Massi Pallarés, R. & Benítez Usher, C. A. (1982). De la distribución de Ixodina (Vander Hammen, 1968) en el Paraguay. Revista Paraguaya de Microbiología, 17, 49–52.
- Minning, W. (1934). Beiträge zur systematik und morphologie der zeckengattung Boophilus Curtice. Zeitschrift für Parasitenkunde, 7, 1–43.
- Nava, S., Mangold, A. J. & Guglielmone, A. A. (2006). The natural hosts of larvae and nymphs of Amblyomma tigrinum Koch, 1844. Veterinary Parasitology, 140, 124–132.
- Neumann, L. G. (1899). Révision de la famille des ixodidés (3^e mémoire). *Mémoires de la Société Zoologique de France*, **12**, 107–294.
- Nuttall, G. H. F. & Warburton, C. (1915). Ticks. A Monograph of the Ixodoidea. Part III. The Genus Haemaphysalis. Cambridge, U.K.: Cambridge University Press.
- Oliveira, P. R., Bechara, G. H., Denardi, S. E., Saito, K. C., Nunes, E. T., Szabó, M. P. J. & Mathias, M. I. C. (2005). Comparison of the external morphology of *Rhipicephalus sanguineus* (Latreille, 1806) (Acari: Ixodidae) ticks from Brazil and Argentina. *Veterinary Parasitology*, 129, 139–147.
- Payne, R. C. & Osorio, O. (1990). Tick-borne diseases of cattle in Paraguay. I. Seroepidemiological studies on anaplasmosis and babesiosis. *Tropical Animal Health and Production*, 22, 53–60.
- Perez, M., Rikisha, Y. & Wen, B. (1996). Ehrlichia canis-like agent isolated from a man in Venezuela: antigenic and genetic characterization. Journal of Clinical Microbiology, 34, 2133–2139.
- Petney, T. N., Andrews, R. H., McDiarmid, L. A. & Dixon, B. R. (2004). Argas persicus sensu stricto does occur in Australia. Parasitology Research, 93, 296–299.
- Quinlan, J. F., Scarone, C. A. & Laneri, J. L. (1980). Cattle tick identification and seasonal variation in infestation rates in Paraguay. *Tropical Animal Health* and Production, 12, 259–264.
- Ribeiro, S. S. (1966). Ixodides encontrados no Paraná. Anais da Faculdade de Medicina da Universidade Federal do Paraná, 9-10, 7-51.
- Ripoll, C. M., Remondegui, C. E., Ordoñez, G., Arazamendi, R., Fusaro, H., Hyman, M. J., Paddock, C. D., Zaki, S. R., Olson, J. G. & Santos-Buch, C. A. (1999). Evidence of rickettsial spotted fever and ehrlichial infections in a subtropical territory of Jujuy, Argentina. American Journal of Tropical Medicine and Hygiene, 61, 350–354.

- Robbins, R. G., Karesh, W. B., Painter, L. E. & Rosenberg, S. (1998). Ticks of the genus *Amblyomma* (Acari: Ixodida: Ixodidae) from white-lipped peccaries, *Tayassu pecari*, in northeastern Bolivia, with comments on host specificity. *Entomological News*, 109, 172–176.
- Robbins, R. G., Deem, S. L. & Occi, J. L. (2003). First report of *Amblyomma humerale* Koch (Acari: Ixodida: Ixodidae) from Bolivia, with a synopsis of collections of this tick from the South American yellow-footed tortoise, *Geochelone denticulata* (L.) (Reptilia: Testudines: Testudinae). *Proceedings of the Entomological Society of Washington*, 105, 502–505.
- Robinson, L. E. (1911). New species of ticks (Haemaphysalis, Amblyomma). Parasitology, 4, 478–484.
- Robinson, L. E. (1926). Ticks. A Monograph of the Ixodoidea. Part IV. The Genus Amblyomma. Cambridge, U.K.: Cambridge University Press.
- Salles Gomes, L. (1933). Typho exanthematico de São Paulo. *Brasil Medico*, **47**, 919–927.
- Silva, L. J. & Galvão, M. A. M. (2004). Epidemiologia das riquetsioses do género *Rickettsia* no Brasil. *Revista Brasileira de Parasitologia Veterinária*, 13 (Suppl. 1), 197–198.
- Szabó, M. P. J., Mangold, A. J., Joao, C. F., Bechara, G. H. & Guglielmone, A. A. (2005). Biological and DNA evidence of two dissimilar populations of the *Rhipicephalus sanguineus* tick group (Acari: Ixodidae) in South America. *Veterinary Parasitology*, 130, 131–140.
- Tonelli Rondelli, M. (1931). Ixodoidea del museo di Torino. Bolletino dei Musei di Zoologia e di Anatomia Comparata della Reale Università di Torino, 41, 1–10.
- Tonelli Rondelli, M. (1937). Ixodoidea. Parte I. *Amblyomma ovale* Koch, *Amblyomma cajennense* Fabricius (sic) e le specie a lor affini nuove o poco note. *Rivista di Parassitologia*, 1, 273–298.
- Tonelli Rondelli, M. (1939). Ixodoidea. Parte II. Contributo alla conoscenza della fauna ixodologica Sud-americana. Rivista di Parassitologia, 3, 39–55.
- Unver, A., Perez, M., Orellana, N., Huang, H. & Rikisha, Y. (2001). Molecular and antigenic comparison of *Ehrlichia canis* isolates from dogs, ticks, and a human in Venezuela. *Journal of Clinical Microbiology*, 39, 2788–2793.
- Venzal, J. M., Guglielmone, A. A., Estrada Peña, A., Cabrera, P. A. & Castro, O. (2003). Ticks (Ixodida: Ixodidae) parasitising humans in Uruguay. *Annals of Tropical Medicine and Parasitology*, 97, 769–772.
- Venzal, J. M., Portillo, A., Estrada-Peña, A., Castro, O., Cabrera, P. A. & Oteo, J. A. (2004). Rickettsia parkeri in Amblyomma triste from Uruguay. Emerging and Infectious Diseases, 10, 1493–1495.
- Walter, G. (1990). Zeckenfunde (Ixodoidea, Ixodiade) aus Paraguay und Peru. Andrias, 7, 169–170.
- Whitaker, J. O. & Abrell, D. B. (1987). Notes on some ectoparasites from mammals of Paraguay. Entomological News, 98, 198–204.
- Wilson, D. E. & Reeder, D. M. (1993). Mammal Species of the World, 2nd Edn. Washington, DC: Smithsonian Institution Press.